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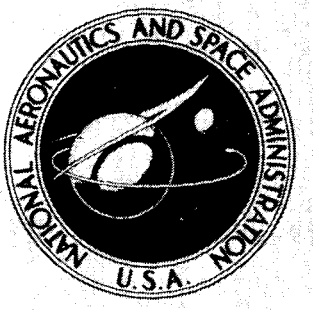

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METABOLIC RATE AND LONGEVITY OF DROSOPHILA

II. THE LONGEVITY AND METABOLIC RATE IN DROSOPHILA MELANOGASTER AT DIFFERENT POPULATION DENSITIES

by A. P. Shcherbakov

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By A. P. Shcherbakov

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METABOLIC RATE AND LONGEVITY OF DROSOPHILA. II. THE LONGEVITY AND METABOLIC RATE IN DROSOPHILA MELANOGASTER AT DIFFERENT POPULATION DENSITIES

A. P. Shcherbakov[1]

The intensity of oxygen absorption in adult Drosophila melanogaster varies with the change in the density of population. With increase of density the intensity of respiration increases. With a density of 2 flies per vessel (30 cc volume), the absorption of O_2 per hour per gram of weight equals 4.13 cc; with a density of 200 flies respiration increases to 5.16 cc O_2. The intensity of respiration changes much less than the duration of life of the flies according to Pearl. The changes of these two factors have an entirely different character. While the longevity of the flies decreases in both directions from a certain optimal density of population (30-50 flies per vessel), respiration simply increases, though irregularly, with the increasing density.

The effect of population density on length of life in Drosophila melanogaster has been studied by Pearl et al (ref. 1). Placing various numbers of flies in vessels of uniform volume (1 oz) with a uniform amount of food (8 cc) and making a daily mortality count, the authors established a strong dependence between the average length of life and the pattern of fly mortality on the one hand, and population density on the other. Table 1 shows the average length of life for various initial densities. The flies were kept in an incubator at 25°C. The number of flies was different for different densities--from 300 flies at the lowest density to 2000 at the highest. Both sexes were counted together, males and females being equally distributed among the test tubes. /651*

As can be seen from the data in Table 1, the greatest length of life does not correspond to the lowest population density. There is a certain optimum density (more likely, range of densities) at which length of life is greatest. Under the conditions of Pearl's experiments, this density was approximately equal to 35 to 55 flies per vessel. On both sides of this optimum density, length of life decreases. When the density is reduced to 2 flies per vessel, length of life decreases from 40 days to 27. When density is increased, length of life is curtailed even more severely; thus, at a density of 200 flies per vessel it was equal to only about 12 days. It is interesting that further increase in density, to over 200 flies per vessel, does not much affect length of life.

These facts admit of no doubt, since they are based on an enormous amount of material in all the tests--13,000 flies. It is especially certain since the results obtained in two subsequent series were generally exactly similar.

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*Numbers given in margin indicate pagination in original foreign text.

[1]Department of General Biology of VIEM (All-Union Institute of Experimental Medicine). (Director, Professor E. S. Bauer.)

TABLE 1.

Initial density	Average length of life, days
2	27.31 ± .58
4	29.32 ± .60
6	34.45 ± .65
8	34.20 ± .61
10	36.22 ± .72
12	34.21 ± .61
15	37.92 ± .66
20	37.07 ± .55
25	37.47 ± .49
35	39.34 ± .67
45	37.46 ± .51
55	40.34 ± .53
65	35.25 ± .45
75	32.34 ± .46
85	30.10 ± .36
95	27.17 ± .36
105	24.20 ± .32
125	19.60 ± .28
150	16.17 ± .24
200	11.93 ± .20

At present we cannot explain this strong effect of population density on length of life. In Drosophila the mechanism of effect of this factor is so far completely unstudied. And if it is easy to imagine how overcrowding of organisms in a small volume can affect the most varied aspects of vital activity, it is much harder to explain decrease in the length of life when density is reduced. /652

The present study investigated the intensity of metabolism in Drosophila at various population densities. We thought it would be interesting to compare the intensity of metabolism with data already available on length of life. As was shown in Communication I (ref. 2), length of life under known conditions is in strict dependence on the intensity of metabolism. Whether this ratio is preserved at different population densities it was the aim of the experiments described below to discover.

Methods

The experiments were conducted on adult Drosophila melanogaster. The flies belonged to the line brought from Nal'chik (northern Caucasus), bred many years in the laboratory.

To ensure that the densities would correspond to those at which Pearl kept his flies, test tubes of the same size were used. The nutrient was the usual kind: potato with raisins and agar; the surface of the nutrient was washed with yeast. The flies were kept in an incubator in darkness. Temperature in the incubator throughout the experiments was $25.7^{\circ} \pm 0.07^{\circ}$ C. Fluctuations were rather large, amounting in some cases to two degrees. The nutrient was changed daily. Two series were run. In the second series the surface of the nutrient was covered with finely divided pieces of filter paper. The paper was intended to reduce moisture, which in the first series often caused the flies to drown. However, the use of the paper palpably worsened feeding conditions for the flies, and the length of life in the second series was considerably less than in the first series.

Metabolic intensity was determined from oxygen absorption. Two methods were used. For low densities, Fenn's differential respirometer (ref. 3) with slightly modified chambers was used. The modification was that the chambers were cylindrical in shape with a false bottom containing a row of perforations near the actual bottom. The flies were placed in the upper half of the chamber; in the lower half, 5 percent sodium hydroxide was introduced through a lateral tube to absorb carbon dioxide. One of the respirometers was particularly sensitive, capable of recording the oxygen consumption of two flies. At high population densities, respiration was determined with a Warburg manometer. The same chambers were used. In the great majority of experiments, oxygen

absorption proceeded at a constant rate, i.e., a graphic plot of the course of the experiment yielded a straight line. This shows that the experimental conditions (absence of food, etc.) did not affect, at least during the experiment, the normal course of metabolism. All experiments which did not show a rectilinear plot for oxygen absorption (and these were very few) were thrown out. All experiments involving respiration were conducted at 26° under diffused lighting.

Before the experiments, the flies, lightly anesthetized with ether, were weighed on an analytical balance. A few minutes after being placed in the respirometer chamber they all reacted and began to move normally. Another 45 min to 1 hr elapsed from this point until recording of readings began. Judging from the rectilinearity of the respiration plots, all aftereffects of the anesthesia had worn off by this time. The results of the experiments are expressed in cubic centimeters of O_2 per hr per gram live weight of flies. Respiration was determined for males and females together.

Results

Based on the data on length of life given in table 1, five population densities were chosen: in the optimum range, 40 flies per test tube; below the optimum, 2 and 10 flies per test tube; and above the optimum, 100 and 200 flies per test tube. During the experiments with respiration, the flies were kept /653
at the same densities as in the test tubes with the nutrient. The basic results are given in table 2. The first row gives the population density; the second, the average absorption of oxygen per hr per gram live weight in cubic centimeters and the mean error; the next, the extreme limits of variation of oxygen absorption in individual experiments; and the last, the number of determinations made.

Table 2 summarizes respiration data for both series of flies, since there was no difference in the results obtained for the first and second series.

Examination of these data first of all reveals that the intensity of respiration increases very slightly with change in density from 2 to 200 flies per test tube. If a purely statistical approach is used, an actual difference exists only between the respiration values for these two extreme densities. The difference between oxygen absorption at a density of 2 (4.13 cc) and at a

TABLE 2. ABSORPTION OF O_2 BY DROSOPHILA MELANOGASTER AT VARIOUS DENSITIES; TEMP = 26°C.

Density: number of flies	2	10	40	100	200
Average O_2 absorption in cc/hr/g live weight.....	4.13 ± .20	4.65 ± .17	4.62 ± .19	4.71 ± .20	5.16 ± .25
Variation in O_2 absorption in individual experiments..	3.00—6.46	2.86—5.70	3.05—5.58	3.45—6.00	4.52—6.59
Number of determinations.....	21	20	18	14	9

density of 10 (4.67 cc) lies within the limits of error. The same is true in the case of other differences.

Thus, on the basis of Table 2 we may conclude that the intensity of respiration changes much less than average length of life with changes in population density. These changes are also different in character: length of life, beginning with the lowest density, increases with increased density up to a certain limit, and then decreases as density continues to increase. Respiration, however, is weakest at the lowest density, remains constant at densities from 10 to 100 flies per test tube, and again increases as a density of 200 approached.

If we should attempt to compute Rubner's constant from tables 1 and 2, i.e., the product of length of life times metabolic intensity, it appears that the value of the constant would not be the same at different densities. It would be greatest at a density of 40 flies per test tube, and would decrease as density increased or decreased. We will refrain here from considering absolute values of Rubner's constant, since we would have to compare our data on respiration with length of life data obtained from Pearl's experiments. Not to speak of the temperature difference, which did exist (25° and 26°), there may be other discrepancies in the conditions under which the flies were kept. Unfortunately, we were unable for technical reasons to conduct a special series to determine average length of life simultaneously with the experiments on respiration. Orientation data on average length of life could only be obtained on the basis of a count of the mortality of the flies used in the respiration experiments. At densities of 2 and 10 flies per test tube, the amount of material was too small to serve as reference data. As for densities of 40, 100, and 200, the results obtained were identical with those of Pearl, although curtailment of length of life with increased density was not as sharply defined.

The rather larger number of oxygen absorption determinations made in the /654
present study (82 experiments in all variants) makes it possible to touch briefly on a side issue which, though not directly relevant to the theme of this paper, nonetheless is of interest. This is the question of the intensity of respiration in flies of various ages. The experiments on respiration at various population densities were set up in such a way that the consumption of oxygen by a given quantity of experimental material was determined for a second time after a known time interval. Thus, the determinations covered the entire life span from the first days after emergence from the pupa to old age. Since respiration intensity was determined in Drosophila in an active state, as in the case of other organisms, the results varied widely from experiment to experiment. The data in table 2 give an idea of the range of variation. If we had only a small number of experiments on flies of different ages, these fluctuations might distort the effect of age on respiration intensity. In order to avoid this, we decided to consolidate the data of all five series of respiration intensity experiments in one graph. In those cases where several determinations were available for one and the same age, the average was used. The values thus obtained are shown in figure 1. In this graph, the horizontal axis gives the age of the flies in days starting with emergence from the pupa; the vertical axis shows oxygen absorption in cc per hour per gram live weight. It should once more be emphasized that the individual points in figure 1 are not equally weighted, since they are based on different numbers of experiments.

As was expected, the points in figure 1 are well scattered. However, the general character of their distribution quite clearly indicates a tendency for intensity of respiration to decrease with age. This becomes still clearer if instead of using the respiration intensity for each day we take the average over a period of several days. The triangles indicate such average respiration intensity values for successive five-day periods. It is still too soon to say anything at this time about how respiration intensity changes with age; this will require the accumulation of a broader base of material. Whether respiration intensity begins to decrease from the first days of the life of adult flies, or whether in the beginning there is a period of constant intensity, this is hard to say. The only thing which is beyong doubt is that in the flies respiration becomes weaker with age and that this begins to be apparent long before the culture dies off.

Conclusions

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At different population densities, the absorption of oxygen by adult Drosophila melanogaster varies. Respiration intensity increases with increased density. If at a population density of 2 flies in a vessel of approximately 30 cc, O_2 absorption per hour per gram live weight is equal to 4.13 cc, an increase in density to 200 flies intensifies respiration to 5.16 cc O_2.

Intensity of respiration changes much less than average length of life based on Pearl's data. Furthermore, the changes of these two values differ in character: while length of life decreases on either side of a certain optimum population density (30 to 50 flies per vessel), respiration intensity simply increases, albeit unevenly, with increased density.

Thus, if the product of average length of life times metabolic intensity (Rubner's constant) is computed, it will be found to differ for each of the five population densities investigated by the present study. The greatest value of

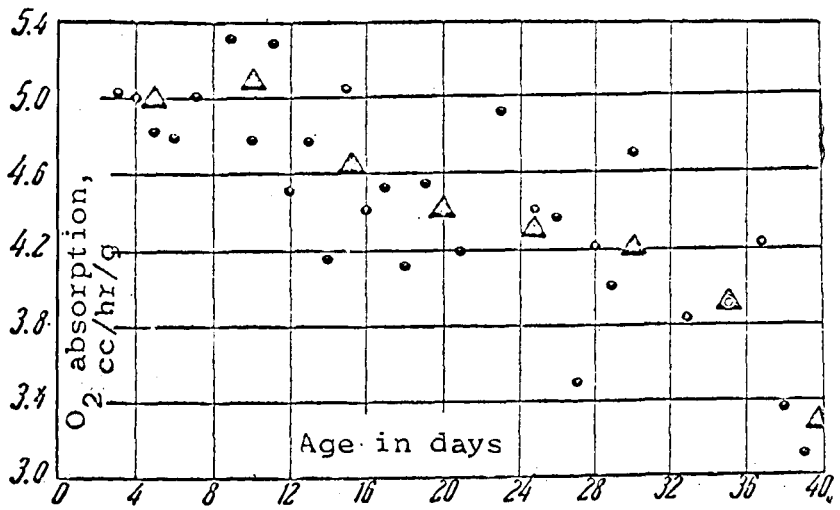

Figure 1. Respiration intensity vs age from all five series of experiments at different densities.

this product will be that obtained for an average density of 40 flies per vessel.

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